

TRACE FOSSILS FROM RHAETIC SHORE-FACE DEPOSITS OF STAFFORDSHIRE

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ABSTRACT. The basal Rhaetic deposits of the Needwood Basin, Staffordshire, are of sandstone facies, in marked contrast to the well known bone beds and dark shales of the transgressive Westbury Formation which crop out elsewhere. The ochreous yellow sandstones contain abundant but poorly preserved bivalves (*Eotrapezium* sp.) together with an extensive ichnofauna which is dominated by *Pelecypodichmus* but also includes *Arenicolites*, *Kouphichnium*, *Palaeophycus*, *Planolites*, and *Rusophycus* in addition to various other trails and burrows. Although this trace fossil assemblage suggests an environment which could range from non-marine to marginal marine, the latter environment is indicated for these shallow water sands by the presence of the marine *Eotrapezium*. The Needwood trace fossils and facies show close similarities to the German Rhätsandstein, a sequence of offshore and marginal marine sandstones.

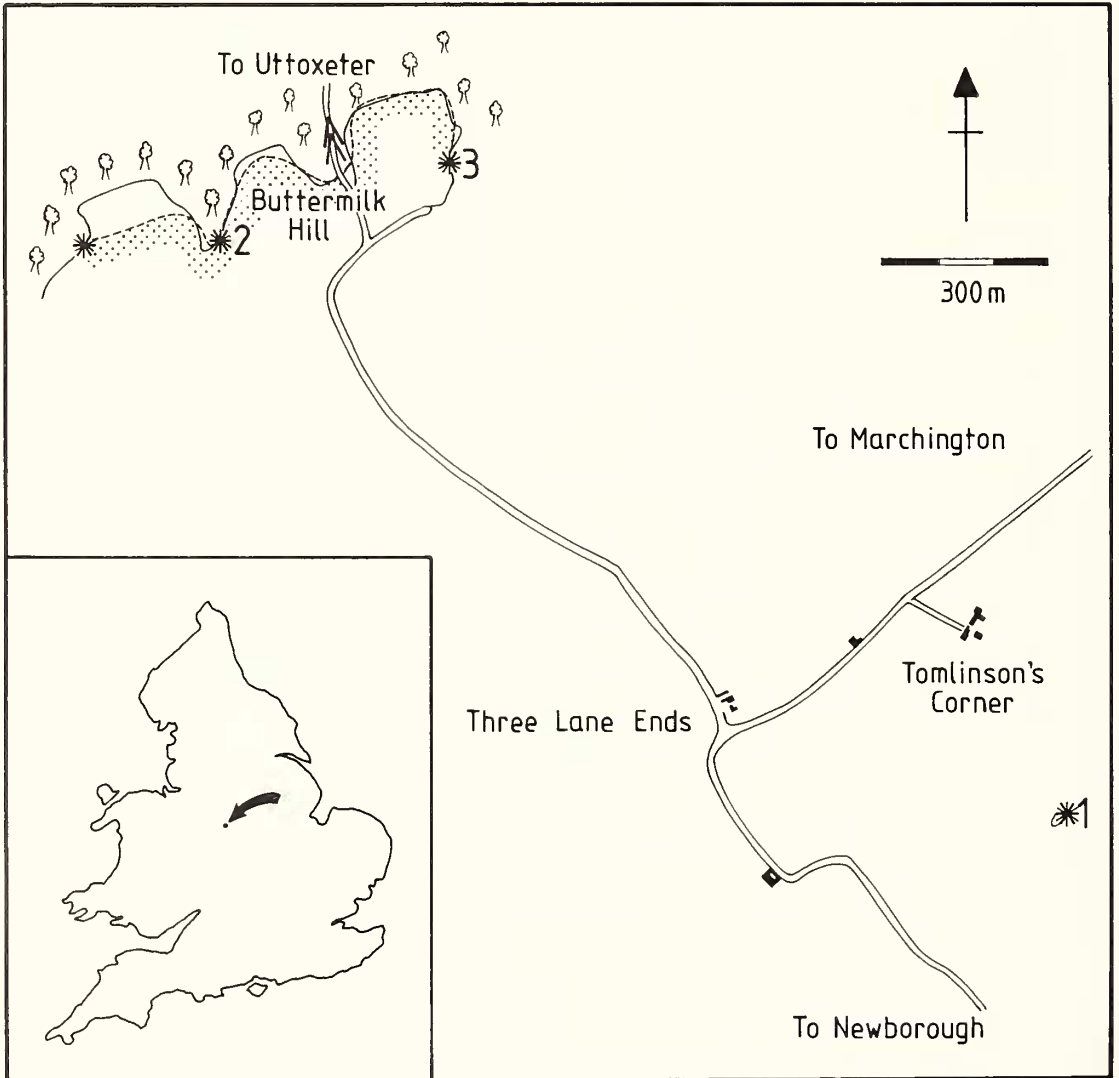
THE presence of trace fossils in the uppermost Triassic rocks of Needwood Forest, an area of high ground to the west of Burton-on-Trent, Staffordshire, was first noted by Molyneux (1869) who recorded the 'tracks of annelides' in the basal sandstones of the Rhaetic succession. Molyneux's observations were cited in the Burton-on-Trent memoir by Stevenson and Mitchell (1955, p. 65) but not enlarged upon further. In 1975 one of us (A.D.W.) collected a variety of trace fossils from this horizon and presented the preliminary findings at the annual meeting of the Palaeontological Association, held that year at Newcastle. Of particular interest was the occurrence of the abundant trace fossil *Pelecypodichmus* along with moulds of bivalves for although these traces had been interpreted by Seilacher (1953) as being the work of bivalves (and hence his name *Pelecypodichmus*), no body fossils corresponding to the traces had previously been found which, as pointed out by Hallam (1970, p. 195), is the usual situation. Bromley and Asgaard have since reported that radiographs have revealed bivalve body fossils in beds containing *Pelecypodichmus* in the Trias of East Greenland (1979, p. 45), while Broadhurst *et al.* (1980, p. 646) and Eagar *et al.* (1985, p. 130) have figured *Carbonicola* in association with escape shafts and *Pelecypodichmus* from the Upper Carboniferous of northern England. A second trace of interest was a problematic one and consisted of some paired impressions (2.5 mm long) which were interpreted as being produced by the appendages of one limb of an arthropod. As there was no sign of the other limb, and no indisputable track sequence, this interpretation was uncertain and suggestions elicited from Association members ranged from claw traces of dragonfly naiads to the impressions of ostracode valves. The collection of additional material now enables a satisfactory explanation for these tracks to be given.

GEOLOGICAL SETTING

The bed rock of Needwood Forest consists predominantly of the red 'Keuper Marl' of the Mercia Mudstone Group, which contributes economically to the district firstly through the contained Tutbury Gypsum horizon, extensively mined under the north side of the Forest, and secondly in the contribution of its ground water which, on the east side, blends with that flowing along the Trent corridor to produce an ideal water for the brewing of pale ale at Burton-on-Trent. In addition to the Keuper Marl, the Triassic succession of Needwood Forest is capped by two outliers of Rhaetic age in which the Tea Green Marl (Blue Anchor Formation) is overlain by Rhaetic Beds

(Penarth Group), the lower part of which is correlated with the Westbury Formation by Warrington *et al.* (1980, p. 41).

Structurally this succession is in the centre of the Needwood Basin where the beds are essentially horizontally disposed so that the highest ground is underlain by the highest parts of the succession. Exposure is very poor, generally being confined to old marl pits, for not only is the area heavily covered by drift, but the Mercia Mudstones and the Rhaetic shales are soft and readily weathered. The basal deposits of the Westbury Formation take the form of variably bedded fine grained ochreous weathering soft grey sandstones which are nevertheless hard enough to form a well defined



TEXT-FIG. 1. Map showing localities (asterisked) from which the fossiliferous material was collected from the base of the essentially horizontal Rhaetic succession. The broken line indicates the junction between the basal Rhaetic sandstones (stippled) of the Westbury Formation and the underlying Tea Green Marl (Blue Anchor Formation) along the wooded north-facing scarp of Needwood Forest. Inset map indicates the location within central England.

escarpment on the northern edge of the Forest. Sections logged by Molyneux (1869, p. 172) record up to six feet of this sandstone and although many of the outcrops available to him were overgrown when the area was mapped by Stevenson and Mitchell (1955), the rock is still visible in rather scrappy exposures in their north-western outlier (1955, p. 63). The trace fossils described herein are from these basal sandstones, the best material coming from the three localities indicated in text-fig. 1.

Locality 1 (SK12182709) is an old marl pit 400 yards (370 m) SSE of Tomlinson's Corner Farm and some 2 miles east of the Bagot's Park borehole (Stevenson and Mitchell 1955, p. 66). As was noted by these authors, the pit shows 'about 2 ft. 6 in. of fossiliferous sandstone resting on Tea-green Marl. The sandstone yielded "*Pullastra*" *arenicola* Strickland.' The new material was collected in 1975; the present sandstone outcrop is limited to small exposures in tree roots at the edge of the pit.

Locality 2 (SK10632813) is at the head of a small valley cutting the scarp edge 300 yards (275 m) to the west of Buttermilk Hill. The exposed section here shows the uppermost 10 m or so of the Blue Anchor Formation at the top of which is a 3 cm grey-green clay immediately underlying the sandstones of the Westbury Formation. Only the basal half metre of the latter is exposed and consists initially of thinly bedded, rippled, and undulating fine sandstones, typically of half centimetre thickness but with lenses of up to 3 cm; 22 cm above the base is a thicker (6 cm) sandstone succeeded by thin flags (2 cm or so) to complete the 53 cm of exposure. This locality yielded some very fossiliferous material, most slabs being collected from or slightly above the thicker sandstone, the upper surfaces being rippled and with bivalve moulds, the lower surfaces with *Pelecypodichmus*, usually on a thin clay seam of up to 5 mm in thickness. Ripple orientation is extremely variable with one orientation of 135° T being succeeded by one of 42° T on the overlying slab (see below).

Locality 3 (SK11072827) is adjacent to a spring some 200 yards (180 m) east of Buttermilk Hill where the junction of the Blue Anchor Formation and the Westbury Formation is seen in a thin sequence of strata. Exposed above the mudstones of the Blue Anchor Formation are some 35 cm of fine grained sandstones. These are for the most part thinly bedded, 1–2 cm in thickness and again separated by very thin shale partings, but at the top of the exposure sandstone units of 4, 3, and 5 cm were recorded. Once more the upper surfaces are rippled and from the lower surfaces *Pelecypodichmus* protrude down into the sticky clay or shale partings.

The sandstones and their sedimentary environment

The sandstones are formed from well-sorted yellow-grey micaceous quartz sand, typically of very fine grain size but grading to fine sand and occasionally medium sand size. One 3 cm thick sandstone unit shows a distinctly coarser lower surface with scatters of 0.5 mm quartz grains and cavities of up to 5 mm in size from which clasts of mudstone, sand, and carbonate have been weathered out. The yellow-grey sediment is commonly iron stained to a greyish or dark yellowish orange, with lower surfaces and joint faces not infrequently encrusted with brown iron oxides; sparse scatters of carbonaceous fragments of up to 1 mm in length occur infrequently in the sand.

On the upper surfaces the ripples are symmetrical and low crested (Pl. 49, fig. 2) with ripple crests peaked or rounded in roughly equal proportions. In most cases the crests are formed of the finer sediment although on the specimen noted above the upper surface shows very variable grain size, and has abundant medium sized quartz grains on the crests with patches of finer sand on the slopes of the troughs. The ripples are generally straight or slightly sinuous and bifurcate in places. Preserved ripple height varies from 5 to 12 mm, and ripple length from 40 to 110 mm; ripple indices vary between 6 and 9. In some specimens ladder ripples, with wavelengths ranging from about 25 to 70 mm, are preserved between the main ripple sets (Pl. 49, fig. 3). These features all indicate a wave origin for the ripples, with the ladder ripples providing evidence of emergence in this shallow water beach environment.

In cross-section, the coarse units are dominated throughout by bioturbated ripple and parallel cross-lamination (Pl. 49, fig. 1). The cross-laminations occur in troughs, some of which are narrow and well defined, with steep foreset laminae. Other troughs are broader, and the cross-laminae are

long, and nearly parallel to the base of the trough. Parallel lamination is also seen below the troughs or below low ripples in some specimens. In terms of the categories of wave generated sediments described by de Raaf *et al.* (1977), the sandstone units show some features of the M_2 (lenticular beds) along with the S_1 (parallel and cross-laminated sandstones). The units are from 1 to 6 cm thick with a grain size of very fine to medium, which falls into the M_2 category, but the parallel lamination is an important structure within the units and corresponds to the S_1 patterns. The mud flasers of the M_2 are moreover essentially missing, the thin clay horizons being on true bedding surfaces which serve to separate the sandstone units. The M_2 and S_1 lithotypes indicate, respectively, moderate but continuous wave action and conditions of considerable wave activity. Parallel and cross-lamination and symmetrical ripples occur in submerged and emergent sand bars lying a little offshore (de Raaf *et al.* 1977, p. 479), in an environment periodically sufficiently sheltered to allow not only bioturbation but also the accumulation of argillaceous seams.

Bioturbation is clearly seen in cross-section (Pl. 49, fig. 1) with some horizons heavily disturbed by burrowing. Vertical escape structures are observed breaking through thicknesses of up to 25 mm of cross-laminated sand from the more intensively burrowed horizons.

The sedimentary structures on the lower surfaces also include the impressions of symmetrical ripple marks, although these are much less common than the ripples on the upper surfaces and are present on only two of the sixteen slabs collected from locality 2 for their well preserved trace fossils. The ripple wavelength ranges from 60 to 82 mm, the mean of 69 mm in a sample of 6 being very similar to that of the upper surface with a mean of 65 mm in a sample of 29; the ripples are, however, much lower. These ripples are simply the impressions of those on the upper surface of the underlying bed, with the subdued form resulting from the muddy horizon coating the ripples below and the subsequent burrowing of the bivalves down into this mud. The apparent ripple index of up to 18 for these shallow ripple impressions should not therefore be interpreted as an indication of the development of current ripples. It is, however, of interest that there is a relative difference of 70° and 75° in the ripple orientations of the lower and upper surfaces of these two slabs, showing again the marked variation noted above from the outcrops.

Several bed bases display abundant tool marks in the form of small, shallow groove marks, 0.4 mm wide and 2–10 mm long. On any particular surface, these tool marks generally show two dominant directions and they are frequently interspersed with, and cut by, small burrows and other trace fossils.

BODY FOSSILS

The only body fossils present in the sandstone are the bivalves alluded to as '*Pullastra arenicola*' Strickland by Stevenson and Mitchell (1955, p. 66). Strickland, however, never figured this species; there are no type specimens; and as his original description (1843, p. 17) is too generalized to be diagnostic, the name would appear to be unusable. No figures of Strickland's species have been traced prior to those of Phillips (1871, pl. 7, figs 6–12) but these show a wide range of shape and

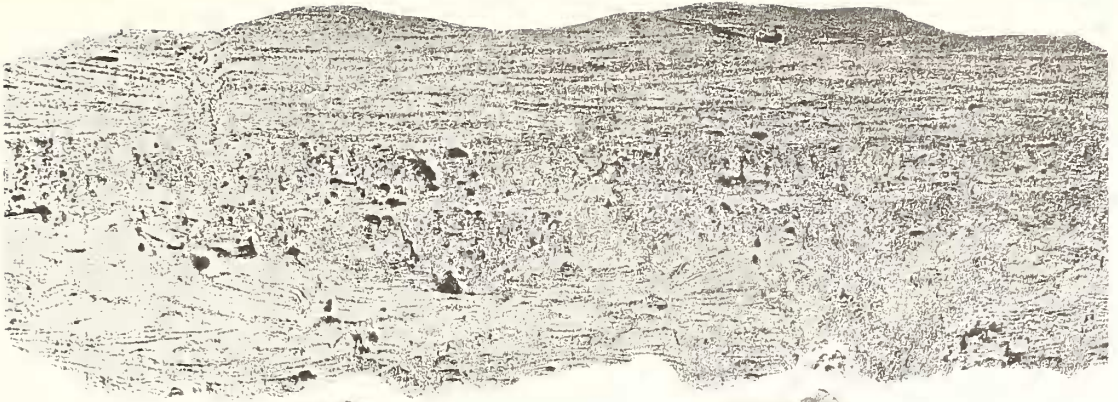
EXPLANATION OF PLATE 49

Fig. 1. Vertical section through a block of sandstone showing ripple and parallel cross lamination with escape structures, and two heavily bioturbated bands across the middle with abundant *Arenicolites* burrows. SM.X.8948. Locality 1. $\times 0.8$.

Fig. 2. Upper surface of sandstone block showing ripples, the internal moulds of *Eotrapezium* (SM.X.8951), paired pits marking the surface expression of *Arenicolites* burrows (SM.X.8953) and a broad ridge trail (SM.X.8955). Locality 1. $\times 0.5$.

Fig. 3. Ladder ripples on the upper surface of a sandstone block. SM.X.8960. Locality 2. $\times 0.5$.

Figs. 4 and 5. Small sandstone block from Locality 1. $\times 1$. 4, lower surface of block showing the close association of *Eotrapezium* valves (concave) (SM.X.8966) with convex hyporeliefs of *Pelecypodichmus* (SM.X.8968). 5, lateral view of this block showing *Eotrapezium* sp. in life position in a burrow (SM.X.8970).



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structure. It would appear best to refer the forms in the sandstone to *Eotrapezium* sp., a small bivalve present in mudstones of this age which could probably leave similar moulds in sandstone (Dr H. Ivimey-Cook, personal correspondence). Variations in outline and proportions do exist and it may well be that more than one species is present; but the specimens, although numerous, occur in the form of very poorly preserved moulds which simply indicate overall shape and, on the external moulds, the presence of concentric growth lines. The convex internal moulds give no indication at all of the form of the hinge structures.

The moulds, ranging in length from 3 to 11 mm, occur both on the upper and lower bedding surfaces and within the body of the sandstones. Those on the upper surfaces are scattered across the troughs of the rippled sand surface as disarticulated valves. The overwhelming majority are in the form of convex internal moulds with only the occasional concave external mould; the ratio of 22:1 counted in the ripple trough of one slab appears fairly typical. One upper surface is unusual in displaying the concave impressions of the external dorsal hinge region of half a dozen articulated shells in addition to the flat lying disarticulated valves.

Disarticulated valves, equally poorly preserved and with the same convex up orientation are found on bedding surfaces within the sandstone units; the valves of one individual both lie flat on the surface, indicating entombment in the sediment before decay of the ligament. Occasional specimens are seen within the body of the sediment orientated perpendicular to the sediment surface in life position (Pl. 49, fig. 5).

On the lower surfaces the disarticulated valves are preserved essentially as concave external moulds, i.e. with the valves again orientated convex side up. While such surfaces may be covered with these moulds and lacking *Pelecypodichnus* traces, and other surfaces covered with these trace fossils but lacking bivalves, *Eotrapezium* and *Pelecypodichnus* were found together on ten out of the sixteen slabs from locality 2. These were sometimes very closely associated (Pl. 49, fig. 4), although the relative proportions of the shells and the traces varied considerably.

Thus apart from the abundance of bivalves and *Pelecypodichnus* on the opposite surfaces of the sandstone units, this preservation of the two on the same surface and the clear evidence of burrowing through the sand provide abundant circumstantial evidence that the *Pelecypodichnus* traces were the product of these bivalves burrowing down through the sand until the underlying clay horizon was reached.

TRACE FOSSILS

A range of trace fossils was observed in the sandstone units. These indicate a diverse fauna moving over the surface of the sand (*Kouphichnium*, groove and ridge trails of various kinds), living within the sand (*Arenicolites* and bivalve escape burrows), and living temporarily, if not continuously, at the lower surface along the sand-clay interface (*Palaeophycus*, *Planolites*, *Rusophycus*, and small trails).

EXPLANATION OF PLATE 50

Fig. 1. *Kouphichnium* trackway (SM.X.8971) trending obliquely across a ripple trough (the two partially preserved ripple crests cross the top and bottom of the figure), with an indeterminate track of sand mounds pushed away by some appendage extending to the right just above the middle and an oblique angular furrow (SM.X.8972) terminating in an oval structure to the left. Locality 2. $\times 1$.

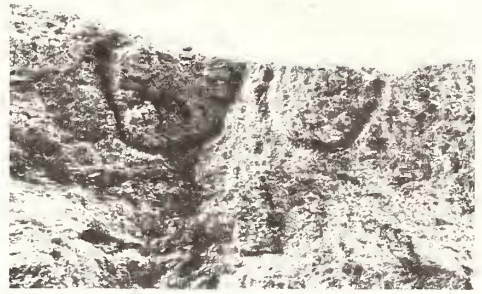
Fig. 2. *Arenicolites* burrows (SM.X.8977, 8) on the broken edge of a sandstone block. Locality 1. $\times 1.5$.

Fig. 3. *Kouphichnium* tracks (SM.X.8973) on the upper surface of a sandstone block clearly showing the impressions of the hind limb. Locality 2. $\times 2$.

Fig. 4. *Kouphichnium* track (SM.X.8981) progressing across a ripple (top right corner to about mid-bottom) in the forms of pits and a median drag mark (right-hand side), then down the bivalve mould-covered longer slope to the left. Here the track is in the form of groups of positive epireliefs best preserved in the top (right-hand) track with a well preserved group of the bottom (left-hand) track recording the basic chevron pattern. Locality 2. $\times 2$.



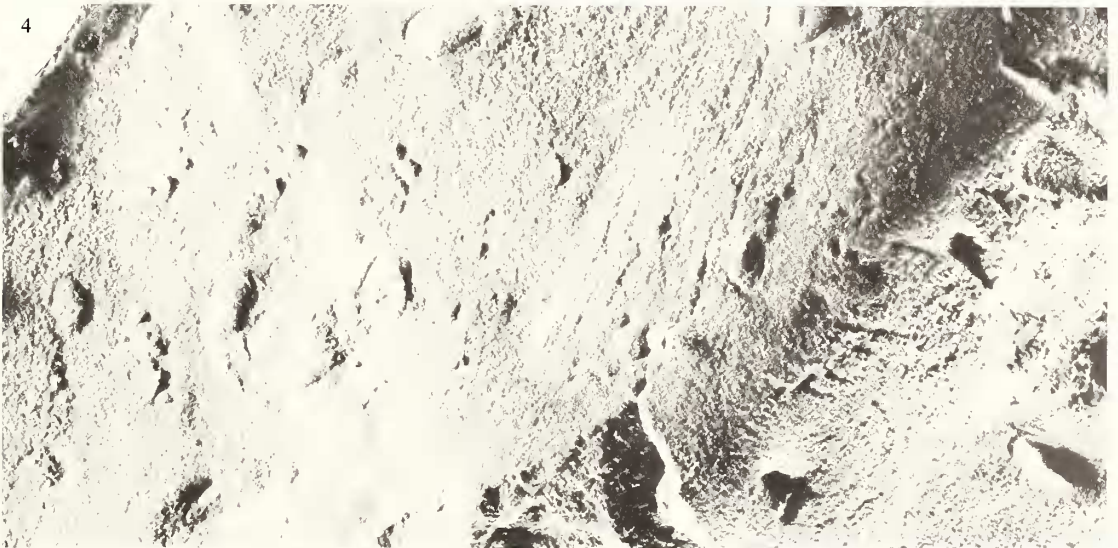
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Ichnogenus *Arenicolites* Salter 1857

Pairs of small pits from 0.8 to 2.0 mm in diameter and separated by about 3 to 10 mm are seen on the upper surfaces of the sandstone slabs. These are the surface expression of U-shaped burrows and are quite common on some surfaces (Pl. 49, fig. 2). One fortuitously broken slab (Pl. 50, fig. 2) shows a vertical section through two of these burrows. They extend from 7 to 10 mm in depth, and transect the laminae of the sand but do not disturb it otherwise. The absence of spreiten indicates *Arenicolites*.

Cut blocks of sandstone show horizons heavily permeated by the *Arenicolites* burrows (Pl. 49, fig. 1), the activities of which were evidently terminated by an influx of sand that contains only the occasional burrow and escape structure.

Environmental interpretation. *Arenicolites* is generally regarded as typical of the shallow marine *Skolithos* and *Glossofungites* ichnofacies, although it is clear that such structures can also be produced in freshwater deposits (see Bromley and Asgaard 1979, p. 43).

Ichnogenus *Kouphichnium* Nopsca 1923

Arthropod-like trackways have been observed on ten of the collected blocks, mostly as poorly preserved trackways (Pl. 50, fig. 1) with only sporadic sharply defined impressions (Pl. 50, fig. 3). The trackways are between 15 and 20 mm wide, and in places show a central drag mark 0.2 to 0.5 mm wide (Pl. 50, fig. 4). The impressions of the tips of the appendages generally take the form of short furrows or pit-like scratch marks. The trackway which crosses the crest of the ripple in Pl. 50, fig. 4 develops into a series of somewhat irregularly disposed groups of 5 to 6 rounded positive epireliefs each up to about 0.7 mm across, arranged *en échelon*, with only a single series on the left side of the trail to produce a chevron shape. The well defined prints are about 3 to 4 mm long and 2 to 4 mm wide (Pl. 50, fig. 3) and show three or four 'toes', with a small mound of sand medianly which has been pushed back by the appendage.

Discussion. The evidence from the rather variably preserved tracks points clearly to *Kouphichnium*, the trackway of a limulid. The chevron series noted indicates the direction of locomotion of the animal as being down this slope of the ripple (Caster 1944, p. 77). The positive reliefs here, as opposed to the negative reliefs elsewhere, are regarded simply as preservation by the compaction of the sand beneath the appendages; the presence of six impressions, rather than five, and their irregular disposition is interpreted as the result of stumbling down the slope; other isolated impressions where some object has pushed into and displaced the sand on a down slope are not uncommon. The toe-like impressions are typical of the limulid hind foot, with its four or five moveable flat spines which serve to push the animal forward; while the central furrow, seen from time to time, is interpreted as a drag mark of the telson.

Environmental interpretation. Limulid tracks are typical of beach and lagoonal deposits, modern *Limulus* migrating from subtidal to supratidal environments with maximum densities of adults at depths of 5 to 6 m on sandy substrates (Rudloe 1979). The classical fossil occurrence is in the lagoonal Solenhofen Limestone (Walther 1904), and other marginal marine records include the Upper Devonian of Pennsylvania (Goldring and Seilacher 1971), the Upper Triassic of Arizona (Caster 1944), and the Rhaetic of Germany (Goldring and Seilacher 1971). Other records of xiphosuran tracks are in sediments interpreted as non-marine in the Upper Carboniferous of England and North America (King 1965; Hardy 1970; Goldring and Seilacher 1971; Chisholm 1983; Eagar *et al.* 1985), the Lower and Middle Triassic of Germany (Goldring and Seilacher 1971; Pollard 1981), and the Upper Triassic of Germany and North America (Goldring and Seilacher 1971). This is further discussed under *Rusophycus* (below).

Ichnogenus *Palaeophycus* Hall 1847*Palaeophycus*, Type A

Small horizontal and subhorizontal burrows, the sediment of which is the same as the matrix, occur as convex hyporeliefs on the bases of the sandstone units, and occasionally as endichnial burrows (Pl. 51, fig. 3). The burrows are roughly cylindrical, 1.0–2.5 mm in diameter and run in straight, slightly curved, or sinuous lines which may branch on occasions, and which disappear upwards into the sandstone. Some surfaces are particularly heavily burrowed by *Palaeophycus*, with specimens crossing and overlapping in a complex mass (Pl. 51, fig. 4).

Discussion. These burrows are smaller than typical *Palaeophycus*, which are generally between 3 and 15 mm in diameter (Häntzschel 1975, p. W89).

Palaeophycus, Type B

Many of the *Palaeophycus* burrows are transversely annulated. These annulated burrows range from 1 to 3 mm in diameter and occur as short, slightly curved or sinuous convex hyporeliefs, extending for up to 2 cm before passing upwards into the sandstone bed. The annulations are spaced at between 0.5 and 0.9 mm intervals and appear to circumscribe the outer surface of the burrows.

Discussion. The annulations are in general poorly preserved, appearing clear and regular in only a few cases (Pl. 52, fig. 1). Typically only a few clear annulations are seen, with the rest of the burrow having a irregular undulose surface. It could be that in most cases the grain size of the sandstone on the lower surfaces is too coarse to preserve the fine detail of the annulations.

Palaeophycus Type A and Type B are differentiated on the basis of having either a smooth or an annulated surface. It may be that these two types simply represent different preservational aspects of the same trace fossil; certainly specimens which show good annulations in one part apparently lack them in another.

Pemberton and Frey (1982, p. 853) recognized five species of *Palaeophycus*, and anticipated a sixth species (*P. 'annulatus'*) characterized by continuous annulations along the burrow. The Needwood specimens would appear to fit into this ichnospecies. While the late Precambrian trace fossil described as *Torrowangea* by Webby (1970, p. 100) shows a comparable narrow diameter (1–2 mm) to the present specimens, that form has more crudely developed annulations with constrictions at 1–4 mm intervals, and the larger and strongly meandering trails suggest that it is the product of a quite distinct trail maker.

Environmental interpretation. *Palaeophycus*, along with *Planolites* (below) is recorded from 'virtually all sedimentary facies' (Pemberton and Frey 1982, p. 849).

Ichnogenus *Pelecypodichnus* Seilacher 1953

(= *Lockeia* James 1879 *nomen oblitum*)

The case for using Seilacher's generic name and regarding James's genus *Lockeia* as a *nomen oblitum* rather than a senior synonym has been put by Hakes (1977, p. 222) and is accepted herein.

Pelecypodichnus is the most abundant trace fossil recovered, and occurs on the lower surfaces of the sandstone units as almond-shaped convex hyporeliefs, widely interpreted as the resting traces of bivalves and, as noted above (p. 412), closely associated with the *Eotrapezium* sp. The hyporeliefs typically measure between 5 and 12 mm long and 4 to 5 mm wide. There is, however, a considerable size range, from 2.5 mm up to 16 mm in length. Some specimens are quite broad, being almost as wide as long (Pl. 51, fig. 1).

Poorly preserved specimens appear to be rather rounded, but most examples show some detail produced by their former occupants. While the resting traces are somewhat irregular, they do show pointed ends and a clear longitudinal ridge-like structure over the deepest part, which may stand

away from the surface by up to 4 mm. Variably disposed furrows may define the ridge laterally, and may be interpreted as impressions made by the valve margins; otherwise the surfaces are smooth.

Discussion. The density of the *Pelecypodichnus* varies enormously, with some slabs showing only the occasional specimen while on others they are very densely packed (Pl. 51, fig. 1); counts of up to 40 within a 5 cm × 5 cm square have been made on this block. Although up to 35 are present within the same area on the block illustrated in Plate 51, fig. 2, the impression here of reduced density is simply a reflection of the smaller size of the majority of the individual traces. As was noted by Osgood (1970, p. 308), although there is no preferred orientation, individual traces may be aligned one behind the other (see also Seilacher 1955, fig. 5; Häntzschel 1975, p. W6). These short chains of up to five or six traces need not necessarily represent the same number of animals but suggest that, particularly where one trace partly truncates another, they may simply reflect a repositioning of a single animal. Thus as far as density is concerned, any data on the traces should not necessarily be interpreted as an indication of the actual numbers of bivalves burrowing down to that surface.

From the two population samples referred to, it would appear that there are different size classes, perhaps representing cohorts of different ages. The lengths of 132 specimens from five blocks were measured to the nearest 0.5 mm and a frequency polygon plotted (text-fig. 2). There may be up to five size classes represented here, with modes equal to 3.5 mm, 5.5 mm, 8.0 mm, 11.0 mm, and 12.5 mm.

Environmental interpretation. *Pelecypodichnus* is a poor indicator of environment since it is known from the distal shelf *Cruziana* Ichnofacies (e.g. Osgood 1970) to the *Scoyenia* Ichnofacies (e.g. Bromley and Asgaard 1979).

Ichnogenus *Planolites* Nicholson 1873

One block has been collected which shows a horizontal *Planolites* burrow (Pl. 52, fig. 3). The burrow is preserved as two essentially perpendicularly disposed short segments, each about 20 mm long and with a diameter of 3.5 mm. One is a roundedly convex hyporelief fading at each end as the burrow passes upwards into the sandstone, and apparently crossing over the other flatly convex hyporelief. The latter has evidently been abraded, so that the contact with the adjacent sand shows the difference between infill and matrix particularly clearly. The infill is finer, better cemented, and paler, lacking the iron-stained particles of the surrounding rock.

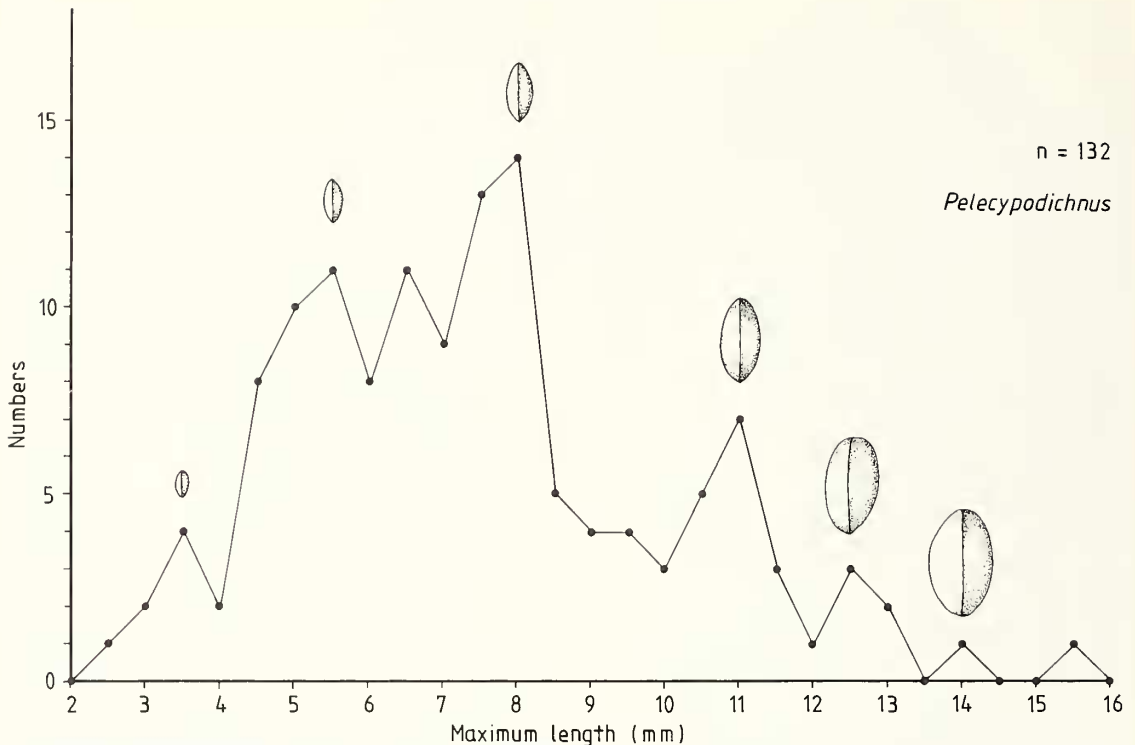
Discussion. The burrow is unlined, with an infill which is structureless, without backfills, and markedly different from the surrounding rock. Thus despite being the sole burrow of this form

EXPLANATION OF PLATE 51

- Fig. 1. Densely packed *Pelecypodichnus* (SM.X.8956) on the lower surface of a sandstone block. Locality 1. × 0.5.
- Fig. 2. Lower surface of a sandstone block largely covered by *Pelecypodichnus* (SM.X.8987) and concave external moulds of *Eotrapezium* sp. (SM.X.8990). Note size and shape contrast of these *Pelecypodichnus* with those of fig. 1. Locality to the west of Locality 2 as indicated on text-figure 1. × 0.5.
- Fig. 3. Endichnial *Palaeophycus* Type A (SM.X.8993). Lower half of the figure is the upper surface of a ripple trough; the *Palaeophycus* is seen medianly emerging on an internal sandstone surface from beneath this and extending towards the top of the figure. Fine ridge trails (SM.X.8994) and bivalve internal moulds (SM.X.8996) also present. Locality 2. × 1.
- Fig. 4. Lower surface of sandstone block dominated by *Palaeophycus* Type A (SM.X.8961). Downward facing internal sandstone surface (top left) has a scatter of external moulds of *Eotrapezium* sp. (SM.X.8964). Locality 2. × 0.5.



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TEXT-FIG. 2. Size-frequency distribution of the lengths of 132 specimens of *Pelecypodichnus* measured on five sandstone blocks.

collected, it clearly falls within the scope of *Planolites* as redefined by Pemberton and Frey (1982, p. 865).

Ichnogenus *Rusophycus* Hall 1853

Several specimens of roughly bilobate convex hyporeliefs are preserved. On one block (Pl. 52, fig. 4), the traces are 18–21 mm wide and 36 mm long. There are two lateral lobes, on either side of a median furrow, each marked by irregular and well spaced obliquely transverse furrows. At the anterior, there is a broad 'head shield' mark, a crescent shaped ridge that cuts across the bilobed shape behind. The buckler is 18–21 mm wide, and 8–9 mm long.

EXPLANATION OF PLATE 52

- Fig. 1. *Palaephycus* Type B (SM.X.8998) showing characteristic annulations, associated with *Pelecypodichnus* (SM.X.9001) on the lower surface of a sandstone block. Locality 2. $\times 2$.
- Fig. 2. Broad ridge trail (SM.X.8955) on the upper surface of a sandstone block (detail of Pl. 49, fig. 2). $\times 1$.
- Fig. 3. *Planolites* burrows (SM.X.9009) seen as a convex hyporelief (mid-field), with a flatly convex segment extending to the right and parallel to the top of the figure from about mid-length of the convex relief. *Pelecypodichnus* resting trace (SM.X.9011) at bottom left. Locality 2. $\times 1.5$.
- Fig. 4. *Rusophycus* (SM.X.9003) with *Pelecypodichnus* (SM.X.9006) and occasional external moulds of *Eotrapezium* sp. (SM.X.9008) on the lower surface of a sandstone block. Locality 2. $\times 0.5$.
- Fig. 5. *Rusophycus* (SM.X.8986) on the lower surface of a sandstone block. Locality 2. $\times 1$.



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One other specimen (Pl. 52, fig. 5) shows only the buckler (25 mm wide, *c.* 12 mm long), associated with a few shallow 'scratch' marks behind.

Discussion. These traces are interpreted as shallow burrows made on a muddy surface by the limulids responsible for the *Kouphichnium* traces described above. The size of the *Rusophycus* (18–21 mm wide) compares well with the *Kouphichnium* track width (15–20 mm). Further, the head shield trace matches the form and curvature of a limulid head shield and is again of the correct size, being as wide as, or wider than, the trackway width.

Rusophycus, characteristic of the distal shelf *Cruziana* Ichnofacies, is normally assumed to be a trilobite trace fossil (Osgood 1970; Häntzschel 1975, pp. W101–102) and typically shows the same characteristics as the present specimens: bilobed, irregularly wrinkled convex hyporeliefs on bed bottoms; occasional presence of head shield markings; association with trackways of the supposed producer. Typical *Rusophycus* is recorded from the Upper Precambrian to the Devonian (Häntzschel 1975, p. W102), and it would not be expected after the extinction of the trilobites in the late Permian. Traces which, like the present ones, are morphologically and ethologically equivalent to *Rusophycus* have nevertheless been recorded from Triassic rocks.

The general problem of trilobite traces of Triassic age has been commented on by several authors. Seilacher (1953, p. 89) referred them to the work of phyllopod crustaceans, while Bromley and Asgaard (1972, 1979) ascribed some examples from Greenland, and Pollard (1985) some examples from England and Scotland, to notostracan branchiopods. Several authors (e.g. Osgood 1970, p. 303; Häntzschel 1975, p. W74; Trewin 1976) attempted to restrict the names *Cruziana* and *Rusophycus* to marine trilobite-produced forms, and to name the non-marine examples as *Isopodichnus*. There are great problems with this approach, since many non-marine and Triassic examples of arthropod-produced traces are indistinguishable from species of *Cruziana* and *Rusophycus* (Bromley and Asgaard 1972, 1979; Frey and Seilacher 1980; Seilacher 1985). The problems in terminology are shown by Häntzschel who himself ascribed a bilobate resting trace from the Upper Triassic of Germany to *Rusophycus* (1975, p. W6). Pollard (1985, p. 283) considers the nomenclatorial problems of *Cruziana*–*Rusophycus*–*Isopodichnus* and prefers to retain the last name for Triassic bilobates, but admits that there are no clear morphological criteria for its identification.

We follow Bromley and Asgaard (1979) in naming the Needwood bilobates as *Rusophycus* on strictly morphological criteria. The specimens from Greenland (Bromley and Asgaard 1972, 1979) and England (Pollard 1985) that were ascribed to notostracans differ from the Needwood specimens in being much smaller, in having well preserved oblique striations on the lobes, and in lacking the crescent-shaped head shield impressions. Closer to the present specimens in this respect are the xiphosurid traces described from the Upper Carboniferous of Northern England by Hardy (1970) and by Eagar *et al.* (1985). These consist of several crescent-shaped casts of the head shield, associated with occasional footprints and telson drag marks, which were found in shallow water, probably non-marine, sandstones associated with *Pelecypodichnus*. Seilacher also described similar bilobates from the marine Rhaetic Sandstone of Pfrondorf, SW Germany, although his figured specimen (1985, p. 233) is a cruzianiform trail rather than a rusophycoid resting trace. He noted the arcuate impressions of the head shield which result from the xiphosurian tendency to burrow in a head-down (prosocline) manner. Further *Cruziana*-like trace fossils, probably made by xiphosurids, have been described from fluvial sequences in the Lower Triassic of South Africa (Shone 1978).

The limulid resting trace recently described by Miller (1982) as *Limulicubichnus* is one which occurs as a shallow concave epirelief on the upper surface of the sand. The tear-shaped outline of this trace is characterized by a poorly defined anterior margin which is ascribed by Miller to the slumping in of sand after burrow formation. Eagar *et al.* (1985) ascribe a selection of xiphosurid resting traces from the Carboniferous of England to *Limulicubichnus*. These specimens are convex hyporeliefs, like the Needwood examples, but they are lunate in shape, mirroring the shape of the xiphosurid prosoma fairly precisely. It would be inappropriate to use the name *Limulicubichnus* for the present examples both in terms of their shape and in terms of their ethological interpretation. The Needwood specimens of *Rusophycus* have a deep frontal definition which reflects the burrowing

of the animal down into the clay horizon, and the infilling of this mould with sand when the burrow was abandoned.

Environmental interpretation. Although *Rusophycus* is normally regarded as typical of the *Cruziana* Ichnofacies (marine: distal shelf), with those of non-trilobite origin noted above of the fresh-water terrestrial environment (*Scoyenia* Ichnofacies), the *Rusophycus* traces produced by limulids indicate a shallow marine to terrestrial environment on the basis of modern limulid distribution, and by comparison with other fossil occurrences (e.g. Miller 1982; Eagar *et al.* 1985).

Furrows

Several slabs show angular furrows with V-shaped profiles, up to 2 mm deep and a width generally between 1.5 and 2.5 mm, scored across the upper surface of the sandstone. The furrows have preserved lengths of up to 80 mm and follow broadly curved shapes, with sand grains heaped up to form an irregular ridge on either side of the furrow. In four examples the furrow ends with an expansion into an oval area 5 mm or so in width. One slab shows a group of furrows radiating from a ripple crest to give the fortuitous impression of an irregular star shaped trace (Pl. 53, fig. 4).

Discussion. These marks are too deep and too irregular in their direction to be tool marks, and were evidently formed by some suspended object, 2 mm or more in width, which ploughed through the sand with some force to leave the V-shaped furrow and to push the displaced sand out sideways. The oval structure shown in Pl. 53, fig. 2 gives a clear indication of the furrow maker changing direction and pushing the sand to the right as it moved to the left and upwards away from the sand surface.

The furrows occur on surfaces with *Kouphichnium* traces, and while the furrows are more deeply impressed than the telson drag marks running between the *Kouphichnium* trackways already noted, they may well have been formed by some such intermittent trace maker. Very closely comparable traces have been recorded from fluvial deposits by Turner (1978), essentially differing only from the Needwood specimens in their larger size (up to 3 mm deep, and with constant widths of between 7 and 12 mm). These traces were tentatively identified as *Scolicia?* and the suggestion made that they could have been produced by snails or bivalves. Similar trails made by modern bivalves have been figured by Schäfer (1972, pl. 17b), Chamberlain (1975, figs. 19.4K, 19.8B), and Hakes (1976, pl. 4, fig. 1b).

Beaded furrow trails

A furrow on the upper surface of one slab is unusual in having a 'beaded' appearance (Pl. 53, fig. 1); three, and possibly six, other furrows may well be of the same form but are indifferently preserved compared with the figured specimen.

The furrow is 1.0–1.2 mm wide and 1.0 mm deep, rounded at the bottom; along each edge is a series of discrete, subspherical lumps with a count of 11 in 10 mm and which apparently alternate on either side. Of 0.6–0.8 mm diameter, they increase the overall width of the trail to a total of 2.4–2.9 mm. The whole trail is 65 mm long, following a slightly sinuous course and shallowing at one end where it seems to pass into a beaded ridge, which may indicate the fading of the furrow and one beaded margin.

Discussion. There are numerous trails on this surface, particularly of the fine ridge trails noted below, several of which have been cut through by this beaded trail. Although the form of the beads is commonly indistinct, this is to be expected as the beads themselves are formed from the same relatively friable sandy sediment as the adjacent surface. This similarity of sediment further mitigates against their having been produced by a sediment ingestor. Where well preserved, the beads appear to be regularly developed, and alternate in position on either side of the furrow. The trail seems to have been formed by an organism ploughing through the surface sediment and displacing fine sand to either side. The beaded appearance was probably formed by motions of lateral limbs or setae, or

by jerking locomotory movements, rather than by any passage of sediment through the body of the organism. Although showing some resemblance to *Chevronichmus* from the Carboniferous of Kansas (Hakes 1976, p. 22, pl. 3), the Needwood specimens are distinct in lacking the continuous V-shaped markings across the furrow that characterize the larger *Chevronichmus*.

Fine ridge trails

On the upper surfaces of the sandstone are convex epireliefs in the form of narrow rounded ridges (Pl. 53, figs. 1 and 5) which range from 0.3 to 0.8 mm wide and have a preserved length typically between 5 and 30 mm. Although some show irregularities, most are essentially straight or gently curving, and tend to fade into the surface at their ends. The ridges do not show branching, but cross in places, either normally or obliquely. In these cases it becomes apparent that the ridge is flanked on either side by a flattened or depressed area, each of about the same width as the ridge itself. The degree of definition of the flanking areas varies from depressions so shallow and poorly defined as to be virtually imperceptible, to depressions sufficiently deep as to be defined by slight ridges along the lateral edges of the depression. At intersections where the depressed areas are well developed, the relative age of the ridges becomes particularly clear as the earlier ridge is cut through by the flanking depressions of the later ridge. The best preserved ridges are in general located in the troughs of the ripples. There is no clear preferred orientation on the floor of the troughs, and although some ridges on the edge of the troughs are aligned normally to the crest, the preserved remains of others trend more or less parallel to or even along the crests.

Discussion. The fine ridges with their flanking depressions and not infrequent cross-overs are probably crawling trails produced on or very close to the surface. The trails are suggestive of those produced by a small snail, possibly one similar to the Recent *Hydrobia* (Schäfer 1972, pl. 18a). No shells of such a snail have yet been found in this sediment, although if their size were comparable to the Recent forms from Strangford Lough whose spires are about 2 mm in height, recognizable preservation would appear to be unlikely in view of the poor preservation of the much more substantial associated bivalves.

Hydrobia is in fact recorded from the Permian fresh water deposits of the Karroo System in Rhodesia, and is ecologically interesting in that the species *H. jenkinsi* Smith is known to have changed from brackish to fresh water habitat within historic time (Cox 1960, p. 187).

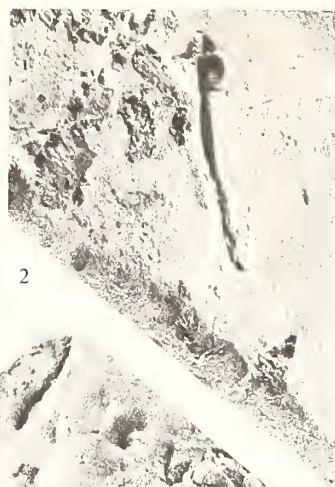
Similar types of trails, but with a width from five to ten times as great, were described by Osgood (1970) from the Upper Ordovician of Ohio. These trails show considerable variation in transverse profile, with one form passing into another (1970, p. 382). In addition to forms with a median ridge, forms with a median furrow also developed, which is what would be expected if the snail were ploughing across the surface of the sand. The use of the foot to draw sand grains inwards to leave

EXPLANATION OF PLATE 53

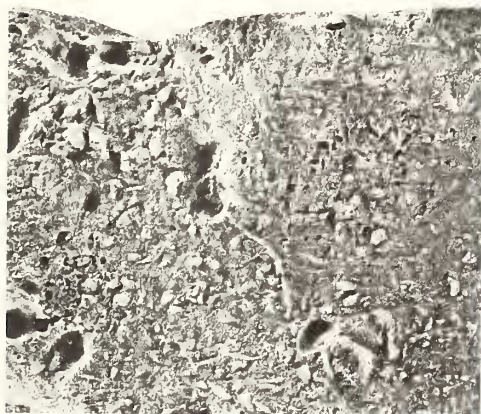
- Fig. 1. Beaded furrow trail (SM.X.9012) cutting across several fine ridge trails (SM.X.9013) on the upper surface of a sandstone block. Internal moulds of *Eotrapezium* (SM.X.9015) also present. Locality 2. $\times 1$.
- Fig. 2. Angular furrow (SM.X.9016) passing down a ripple slope and terminating towards top of figure as the furrow maker changed direction, pushing sand to the right as it moved to the left and upwards away from the sand substrate. Locality 2. $\times 1$.
- Fig. 3. Sinuous fine groove trail (convex hyporelief, SM.X.9019), crossing two external moulds of *Eotrapezium* sp. (SM.X.9020) on the lower surface of a sandstone block. Locality 2. $\times 1$.
- Fig. 4. Angular furrows (SM.X.9026) on the upper surface of a sandstone block, fortuitously arranged in an irregular star shape on a ripple crest and associated with numerous poorly preserved internal moulds of *Eotrapezium* sp. (SM.X.9029). Locality 2. $\times 1$.
- Fig. 5. Fine ridge trails (SM.X.8995), crossing in places, on a ladder rippled upper surface of a sandstone block. Locality 2. $\times 1$.



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the marginal depressions, and then to organize this sand into a median (presumably mucus coated) ridge astern, seems a less obvious type of development.

Some small burrows produced by arthropods are similar in appearance. On modern tidal flats and lake shores, small arthropods such as beetles and mole crickets may produce narrow sinuous burrows beneath the surface of the sand which look like epichnial trails (Chamberlain 1975, figs. 19.3E, 19.4C, 19.5C-E). The trace fossil ‘?Trichichnus’, described by Hakes (1976, p. 36, pl. 10, fig. 2) from the Carboniferous of Kansas appears to be very similar to the Needwood specimens. It is 0.5 mm wide, and occurs as short, fairly straight ‘halbform’ burrows that cross each other.

Environmental interpretation. On the assumption that these traces are produced by gastropods, and as gastropods live in such diverse environments, they have little to contribute environmentally. Although the more complex *Scolicia* type trails have been extensively reported, records of the very thin trails of simple form described here are not known to the authors.

Fine groove trails

Convex hyporeliefs, similar in form and dimensions to the fine ridge trails noted above, are preserved in some abundance on the lower surfaces of several sandstone blocks (Pl. 53, fig. 3). The convex ridges are 0.4–0.6 mm wide, with a rounded profile and observed specimens range from 4 to 15 mm in length. The ridges are straight or curved, less common and generally less well preserved than the morphologically comparable epireliefs; flattened areas lateral to the ridge are suggested by occasional rather poorly defined specimens.

Discussion. Although morphologically closely comparable to the convex epireliefs, these convex hyporeliefs represent the infill of grooves developed on the top of the underlying clay seam or alternatively may be the infill of burrows of a small organism moving along the base of the sand at the clay interface. The latter seems unlikely, as the sediment of the epireliefs does not visibly differ from the adjacent sand on the base of the blocks, and in one sample the ridge contains relatively coarse quartz grains of up to 0.3 mm, again comparable to scattered coarse grains in adjacent sediment. These features would appear to rule out the ingestion of sediment by an organism feeding at the interface. The problem remaining is that the convex epireliefs represent furrows rather than ridges as on the comparable structure of the upper surface. As already noted, the form of similar trails is known to vary in this regard (Osgood 1970, p. 382); in the present case the difference may simply be a reflection of differing substrate lithologies, with the presumed snail leaving a groove on the mud surface and a ridge on the sand surface.

The trails are rare on surfaces with abundant *Pelecypodichnus* and *Palaeophycus* burrows and are typically found on relatively smooth lower surfaces with bivalve moulds and with only the occasional *Pelecypodichnus*.

Broad ridge trail

A single convex epirelief in the form of a relatively broad unbranching ridge is present on the upper surface of a slab with numerous *Arenicolites* burrows (Pl. 52, fig. 2). The epirelief has a low rounded convex profile, width varying from 5.5 to 7.5 mm, and is variably well defined for about 6 cm where it stands out as an arcuate ridge on a ripple slope. Where it crosses the ripple crest definition is poor, but may be traced into the adjacent ripple trough for about 4 cm from one end, mainly by the continuation of the weathered groove at one side, and apparently all the way across the trough at the other end, although the trail is here both ill defined and interrupted (Pl. 49, fig. 2).

Discussion. Where well defined, the ridge is of smoother appearance than the adjacent sandstone as a result of the sand grains being packed more closely and better cemented. Further, where the trail is completely formed there is less mica on the surface; where abraded, mica flakes appear to be as common as elsewhere in the sand surface. This arrangement is suggestive of a smooth lined burrow such as *Palaeophycus tubularis* Hall (see Pemberton and Frey 1982, p. 859). However, there is no

sign of the trace having the cylindrical form of a burrow and it seems to be simply a ridge produced on the sand surface rather than at a clay-sand interface comparable to the *Palaeophycus* hyporeliefs at the sand-clay interface noted above.

Accordingly the ridge appears most obviously interpreted as the trail of a gastropod moving across the rippled sand surface; it may be that the sedimentary characteristics of the well defined parts of the trail resulted from compression and/or mucus secretion from the foot of the animal.

ENVIRONMENTAL INTERPRETATION

The Rhaetic succession of the British Isles has long been regarded as representing deposition in a shallow sea transgressing rapidly across an area of low relief from the south and south-west. In the lower beds of most areas the shale-mudstone facies is important (Audley-Charles 1970, p. 74), so that the most familiar lithologies at the base of the Westbury Formation are those of the Rhaetic Bone Bed and the *Rhaetavicula contorta* Shales. Thus the clean-washed ochreous sandstones at the base of the sequence of Needwood are unexpected, and hard to match elsewhere in the British Isles. Comparisons could be made with the bioturbated sandstones and siltstones at the base of the Williton Member of North Somerset, a unit within the Blue Anchor Formation that immediately preceded the Rhaetic. The trace fossils include *Arenicolites*, *Diplocraterion*, *Muensteria*, *Planolites*, *Rhizocorallium*, and *Siphonites* in addition to several genera of bivalves (including *Eotrapezium*) which together indicate shallow marine conditions (Mayall 1981). Another sandy shoreline facies, recorded only from boreholes along the western margin of the London Platform, is termed the 'Twyford Beds' (Donovan *et al.* 1979, p. 163; Poole 1979, p. 304; Warrington *et al.* 1980). In this last paper, the brief description is of a 'pale arenaceous and rudaceous marginal facies' (p. 41); detailed descriptions of the type 'Twyford Beds' are to be published in the Chipping Norton Memoir referred to in these papers.

The Needwood outcrop is clearly well removed from the London platform, and also the other land areas of low relief in northern England, Wales, the Mendips, and south-west England widely depicted on palaeogeographic maps (e.g. Audley-Charles 1970, Poole 1979), so that these thin sands would appear to have had a more local source.

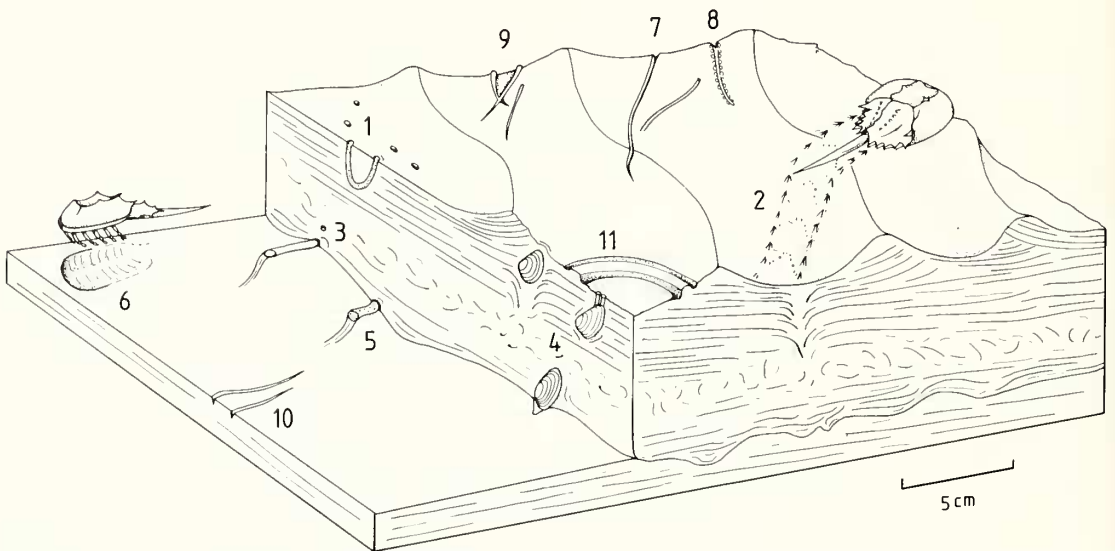
The trace fossils (text-fig. 3) described herein are not too helpful with regard to the depositional environment of the sands as many are well known facies crossers. These include *Palaeophycus*, *Planolites*, and the various ridges and trails. Other trace fossils restrict the ichnofacies to *Cruziana-Scoyenia* (shelf to non-marine: *Pelecypodichnus*) or to *Skolithos-Scoyenia* (marginal marine to non-marine: *Arenicolites*, *Kouphichnium*, and (post-Permian) *Rusophychus*). The bivalve *Eotrapezium*, which is clearly demonstrable as living in these sandy deposits, is a marine form, so that the total fossil evidence points to a marginal marine environment.

A possible analogue of the present sediments and trace fossils is found in the Lower Rhaetic sandstones of south-west Germany. The Rhätsandstein occurs in several deposits around Basel, Metz, Tübingen, Nürnberg, and Coburg. The sandstone is light coloured and fine-grained and it occurs in long trough-like deposits which pass into clay-flaser sandstones and dark sandy clays in places. Both the sandstones and clays contain *Rhaetavicula contorta*, indicating marine conditions (Geyer and Gwinner 1968, p. 51; Aepler 1974).

The Rhätsandstein of south-west Germany has yielded an ichnofauna consisting of resting traces such as *Asteriacites* and *Pelecypodichnus*, small *Cruziana* ('*Isopodichnus*'), '*Cruziana*-like' limulid furrows, limulid tracks (*Kouphichnium*), and U-shaped burrows (*Arenicolites*, and forms with spreiten structures) (Linck 1942; Seilacher 1953, 1955; Goldring and Seilacher 1971; Aepler 1974; Pollard 1981; Seilacher 1985). The Rhätsandstein contains three main facies types, which have been interpreted (Aepler 1974) as elements of a prograding delta sequence which contains evidence of longshore drift, and episodic radial sedimentation during floods. The Needwood sandstones could be compared with either the Schönbuch or the Pfrondorf facies. The Schönbuch facies consists of relatively thin (50-200 mm) sandstone beds with U-shaped burrows, resting traces (*Asteriacites*) and casts of bivalve shells, together with bone beds. The sandstones are regarded as high energy

littoral deposits with sediment input from nearby rivers, particularly in the bone beds. The Pfrondorf facies, which seems most like the Needwood sandstones, consists of thick (several metres) and thin (50–200 mm) sandstone units inter-bedded with mudstones. The thin units are heavily bioturbated, with *Pelecypodichnus*, U-shaped burrows, horizontal burrows and trails, and limulid traces (*Kouphichnium*, 'Cruziana'). This facies has been interpreted (Aepler 1974) as an emergent offshore bar near to the mouth of a major river.

A number of non-marine ichnofaunas (*Scoyenia* ichnofacies: Frey and Seilacher 1980) also show similarities with the Needwood ichnofauna. For example, the Upper Triassic Schilfsandstein of south-west Germany has yielded *Rusophycus* (?notostracan), *Sagittichnus* (?bivalve resting trace), *Pelecypodichnus*, *Kouphichnium*, *Merostomichnites*, *Planolites*, *Biformites* (small burrows), *Cylindricum* (vertical burrows), and various vertebrate footprints and unnamed simple trails (Seilacher 1955; Pollard 1981, 1985). The Schilfsandstein is interpreted (Pollard 1981, 1985) as a deltaic deposit with channel and interdistributary lagoonal facies.



TEXT-FIG. 3. Reconstruction to show the ichnofaunal elements present in the basal Rhaetic sands of Needwood Forest. 1—*Arenicolites*; 2—*Kouphichnium*; 3—*Palaeophycus*; 4—*Pelecypodichnus* (with *Eotrapezium*); 5—*Planolites*; 6—*Rusophycus*; 7—furrows; 8—beaded furrow trail; 9—fine ridge trails; 10—fine groove trails; 11—broad ridge trail.

Another possible non-marine analogue to the Needwood trace fossils is the *Pelecypodichnus-Kouphichnium-Arenicolites* Assemblage described by Eagar *et al.* (1985, p. 127) from the Upper Carboniferous of the Central Pennine Basin. *Pelecypodichnus* occurs in association with the non-marine bivalve *Carbonicola*, and other trace fossils such as *Planolites*, *Cochlichnus*, *Limulicubichnus* ('*Kouphichnium*'), and *Arenicolites*. The environments in which these trace fossils occur are interpreted as shallow non-marine interdistributary bay zones which were periodically flooded during monsoon-like rains and exposed during dry spells.

Thus while the trace fossils in themselves could indicate either marginal marine or non-marine conditions, the presence of marine bivalves suggests that the sandy facies at the base of the Needwood Rhaetic is possibly most clearly comparable with the offshore sand bar deposits of the German Rhätsandstein. In this case the present material gives evidence of the post-Palaeozoic *Rusophycus* (and potentially *Cruziana*) occurring in marine as well as non-marine sediments (cf. Frey and Seilacher 1980, p. 203).

Repository. All specimens figured herein have been deposited in the collections of the Sedgwick Museum, Cambridge.

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